The prominence of temperature in biology

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Biology is temperature-dependent

In addition to adding more of a limiting reactant, one way to increase the rate of a chemical reaction is to add heat. It makes chemicals bounce around faster and so come into contact more frequently[1]. The added energy also speeds reactions by providing the activation energy required for endothermic and even exothermic reactions. All of which is to say, reactions go faster at warmer temperatures. What are the consequences? Let's consider two.

[1] Hmm…are chemical reactions a useful analogy for infected hosts interacting with and infecting susceptible hosts? Let's revisit this later!

Thermal optima

Rates of chemical reactions increase *exponentially* with temperature[2] (Figure 1). As a quick rule of thumb, rates of reaction tend to double with a 10°C increase in temperature. So the rate of reactions, even enzymatic reactions such as those involved in metabolism or muscle contractions or most any other biochemical process, tends to increase like the blue line on the graph to the right.

[2] If you wonder why, look up the Arrhenius equation…yet another exponential model, but this one describes the "rate constant" of a chemical reaction.

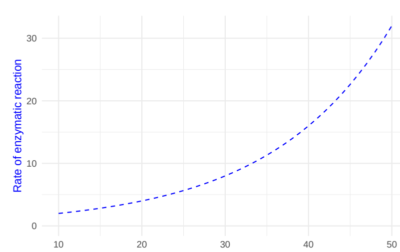

Figure 1

Your intuition is probably quietly screaming at you right now, saying, "yeah, but…!" And your intuition is right. This accelerating relationship between the rate of a reaction and temperature cannot go on forever. At some point, everything catches on fire and you get soot rather than a muscle contraction, right? Even before the fires start our reactions run into other temperature limits. Most biochemical reactions involve enzymes and enzymes eventually fall apart or "denature" at warmer temperatures. (The same can happen to some of the chemical reactants, too.) The pattern of enzymes denaturing as temperature increases is like Hemmingway's statement about how you go bankrupt: "gradually, then suddenly." Let's add a line to the graph at the right showing the proportion of enzymes that are still active (i.e., have not denatured) as a function of temperature (Figure 2).

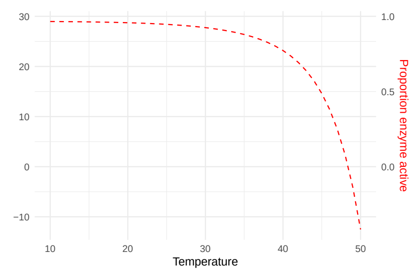

Figure 2

When we put these two processes together (the blue and red lines) we get an overall rate of the reaction (the black line), with a clear peak (Figure 3). This peak corresponds to the temperatures at which the *overall rate* for this hypothetical reaction is maximized. Notice how the curve is asymmetric. Why is that? What do you think might the consequences for the reaction if the temperature is a bit too cold or a bit too warm?

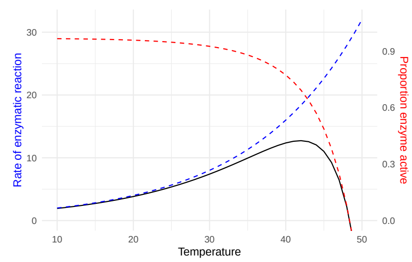

Figure 3: Overall rate of enzymatic reaction

If we were to measure the **thermal performance curve** for a bunch of different biochemical reactions in an organism we would see something pretty striking: they would all look pretty similar. Why is that? Consider what would happen if they were all very different. If they were dissimilar one sort of reaction might proceed efficiently, but another would be creeping along. How could an organism function if, say, all of the reactions causing muscle contractions were working just fine, but those for the neuronal signally were not?! Anyway, the coordination of thermal performance curves means that whole organisms have thermal performance curves, and optima, that stem from, and look like, those of their underlying biochemical reactions[3]. Running speed of a lizard? Yes, it has a thermal optimum. A mosquito digesting a bloodmeal? That, too, happens fastest at a particular temperature.

[3] This is not to say that *everything* needs to have the same optima. Lizards tend to have different thermal performance curves for running speed, digestion, egg production, etc. The more you learn about their biology the more these distinct temperature profiles make sense.

All aspects of biology has some small-ish range of temperatures where it performs best. We humans often do not think about this simply because our physiology works so hard to maintain our body temperature very near our thermal optimum. But trust me, if our core temperature drops a bit, so does our metabolism, just as we would expect[4]. Of course beyond a certain range of body temperatures we become hypo- or hyperthermic and bad things happen.[5]

This is not just hypothetical. Heat waves, especially heat waves combine with humidity[6] to make life miserable for us humans, to the point where some of us, often the most vulnerable, but increasingly larger fractions of the population, can die. And climate change is, of course, making all of this work. We will see not only more heat waves, but more *humid* heat waves. That is important because our primary mechanism of cooling ourselves—sweating—only works when the sweat can evaporate and that is harder under humid conditions. So plant a tree[7], buy a good fan, and stay hydrated.

But this all raises a question: why do organisms have such relatively narrow ranges of temperatures in which they thrive, especially compared to what they can survive? Again, look at that thermal performance curve. Over what range of temperatures do biochemical reactions, all that means in terms of biology, reach their maximum? If they can maintain their body temperatures within that narrow-ish range of temperatures, they can be much, much more efficient (or active, fast, responsive, etc.).[8]!

Temperature-dependent rates of development

Temperature-dependent rates and thermal optima also extend to development. Consider the process of going from an egg to a hatchling to a juvenile to an awkward, gangly pubescent teenager equivalent to a mature adult, or similarly a seed to seedling to small plant to mature plant. All of these steps are the result of a series of chemical reactions, chained together, one after another. Because these reactions tend to go faster at warmer temperatures, the time it takes to get to a particular developmental milestone (e.g., hatching or sprouting) tends to be shorter at warmer temperatures[9]. And while these rates increase more-or-less exponentially over a wide range of temperatures, most organisms do not live, or at least develop,

[4] This also hints at a secret weapon of ectothermic poikilotherms, those things like amphibians and reptiles and some fish that not only get most of their heat from the world around them, but can let their body temperature vary a great deal: they can regulate their metabolism by changing their body temperature. No food? Why not cool down and wait it out? We ridiculous endothermic homeotherms cannot pull off *that* trick!

[5] This hints at something else we need to consider: How do organisms survive in a world where conditions are often *not* ideal? Behavior, physiology, and their environment will all play some role. But more, later.

[6] And poverty, a lack of infrastructure, and loneliness

[7] Shade and evapotranspiration make a big, big difference in local temperatures

[8] Yes, I am overselling this a bit. While the logic holds and there are many examples of temperature-dependent processes from the biochemical (e.g., metabolism) to the organismal (e.g., speed), many other factors also shape temperature-function relationships, such as compensatory adaptations to nutrition. In other words, while this is a good starting point, we need to be cautious about scaling up these temperature-dependent mechanisms too far without care.

[9] Yes, this is true only up to a point.

over a terribly wide range of temperatures. Over this narrower range of temperatures we might be forgiven for thinking that the rate is sort of linear. Let's run with this linear relationship between temperature and rates of development. What are the consequences?

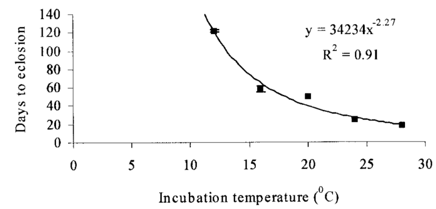

Figure 4: Time to eclosion (hatching) for black legged ticks. From Ogden et al. 2004. Journal of Medical Entomology 41:622-633.

First, if we were to raise, say, ticks (Figure 4) or mosquitoes from eggs at one of a range of temperatures, we would see that the time to some developmental milestone declines rapidly with increasing temperature at first, but that increasing temperatures lead to small and smaller gains in development time. Indeed, this is a hyperbolic relationship where the time to the milestone is just one over the rate of development, which we just noted increases approximately linearly with temperature. That is, $T = 1/d_t$, where d_t is the development rate at temperature t and T is the time to the milestone. Clear? No? OK, let's try an analogy.

Imagine you are driving to the West Side. Let's say it is a 300 mile journey. You could drive the whole way at 60 miles per hour and it would take 300 miles/60 mph = 5 hours or you could drive at 90 mph and it would take 300 miles/90 mph = 3 hours 20 minutes. I you are a very slow driver moving at 30 mph this trip would take 10 hours! A graph of the time it takes to get to your destination, your milestone if you will, follows the same shape as the development graph, above.

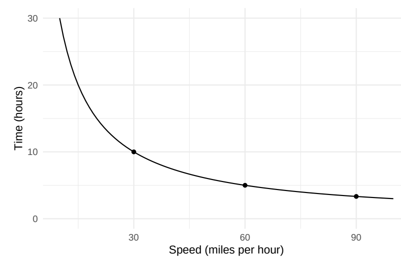

Figure 5: Time to drive to the West Side as a function of speed.

This analogy is important for another reason, because it helps us notice that we do not need to drive (or develop) at a constant rate, but rather accumulate speed (or temperature and development) and thus miles driven (or steps in development) to get to our destination. We might drive at 60 for a bit while we get through Colfax and then floor it on I-90 until we get snarled in traffic near Seattle. Similarly, development might be speeding along on warm days and going slower on cools ones. In biology we call this the "degree-day" model of development[10], where we can estimate the accumulation of temperature as a proxy for the accumulation of development to some developmental milestone.

[10] Sort of like the speed-hour model of travel

This sort of model is very common in farming, but is also very useful for thinking about the ecology of disease vectors. Ticks and mosquitoes take a certain number of degree days[11] to com-

[11] Often above some threshold temperature where there is no development. Zero Celsius is pretty cold, after all!

plete their development into the next developmental stage, lay eggs, or even digest a blood meal. What's cool about this is that we can figure out how many generations we might have in an area as a function of that area's typical temperatures. It can even explain why, say, ticks are not found too far north: it is simply too cold for them to complete their development before they would run out of energy or freeze to death.

And so on...

So there are two ways that temperature ends up playing a prominent role in the biology (and health!) of organisms. Those are big ones, but I bet with some thought we can extend this list a bit more. For instance, temperature differences drive the movements of air and water, meaning they power weather patterns and thus other conditions, such as patterns of rainfall and humidity. Temperature also affects the rates of processes like nitrogen mineralization and nitrification[12], meaning it helps control nutrient availability. Essentially, temperature plays a first- or second-order role in most processes that govern nutrient availability and conditions. So don't be surprised when temperature keeps showing up to the party in this class and the world around us.

[12] And most other biological processes, as we've discussed.